

THE NATURE OF THE TAXON CYCLE IN THE  
MELANESIAN ANT FAUNA\*

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The central contribution of biogeography to general biology is the description of the history of biotas. Aside from its relevance to evolutionary theory, biogeographic history has an immediate significance in population studies: we can expect that the role of individual taxa in ecosystems is influenced both by their geographic origin and by their duration as members of the community. Taxa penetrating from arid source areas will probably fill niches different from those filled by related taxa from moister regions. As a rule, newcomer taxa will undoubtedly affect communities differently from related taxa of long residence. Island biotas derived by radiation of limited stocks show important differences from those derived from more diverse "balanced" stocks, and so on. Of all the major factors that shape community organization, the variables of biogeographic history are probably the least understood. This is due simply to the great complexity of the subject and the tedious nature of its study, which requires revisionary taxonomy as the basic analytical instrument.

The purpose of this paper is to extend an earlier effort (Wilson, 1959a) to synthesize certain information on the zoogeography, speciation patterns and gross ecology of a limited fauna, the ants of Melanesia. In the first report just mentioned, only the subfamily Ponerinae was considered. Faunal sources and expansion patterns of the modern ponerine species were deduced; speciation was shown to be accomplished chiefly by multiple invasions accompanied by major shifts in habitat preferences. In this second study the following groups have been added, following more recent revisionary work by W. L. Brown (1958, 1960, and ms.) and the present author (1957, 1958a, 1959b, c, and ms.): Cerapachyinae, Dolichoderinae, and the myrmicine genera *Pheidole*, *Crematogaster* and *Strumigenys*. These include perhaps 50 per cent of all of the known Melanesian ant species. Not all of the taxa were well enough known to include in all of the analyses; hence, the particular taxa employed are cited with each analysis. Numerical data pertaining to the Asian fauna are based on the catalog by Chapman and Capco (1951), extended and corrected wherever possible by more recent revisionary work. Additional data have been taken from the valuable faunal monographs of Mann (1919, 1921). Emphasis has been shifted somewhat to

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a consideration of certain aspects of the formation of individual faunas, the conditions underlying the origin of expanding taxa, and the interaction of expanding and confined taxa.

Certain expressions have special meanings in these analyses and must be defined at the outset:

*"Central" tropical Asia:* arbitrarily defined as mainland tropical Asia west to and including India and north to and including the "Oriental" portion of southern China, plus Sumatra, Borneo, and Java.

*New Guinea:* refers to the mainland only.

*Expanding taxa:* species extending natively over more than a single archipelago, or higher taxa containing such species. Far-ranging species extending beyond certain arbitrary limits are referred to as Stage-I species (see below).

*Stage-I species, Asia-based:* ranging from tropical Asia, the presumed source area, east to as far as the Moluccas or Micronesia, or beyond.

*Stage-I species, New Guinea-based:* ranging from mainland New Guinea, the presumed source area, to as far as the Moluccas, Solomon Islands, Micronesia, or any combination of these. Species ranging to Queensland, Aru, Manus, Bismarck Archipelago, or Waigeo but not beyond are arbitrarily not classified as Stage-I.

*Stage II and III species:* Species of more restricted ranges interpreted as belonging to other phases of the speciation cycle (see Wilson, 1959a).

#### RELATION OF AREA TO FAUNAL NUMBER

It can be shown that as the area of islands increase, resident faunas of some animal groups logarithmically increase approximately as

$$F = bA^k,$$

where  $F$  is the number of resident species and  $A$  is the land mass in square miles. In the Ponerinae-Cerapachyinae of Melanesia and the Moluccas,  $k$  is approximately 0.7 (figure 1). It is a fact of uncertain significance that  $k$  shows considerable variation among different major animal groups and among different faunas. In the Carabidae and herpetofauna of the Greater Antilles and associated smaller islands it is approximately 0.3. In the breeding land and fresh-water birds it is approximately 0.4 in the islands of the Sunda Shelf (Indonesia) but close to 0.5 in the islands of the Sahul Shelf (New Guinea and environs).

The considerable scatter in the area-fauna measurements of the Ponerinae-Cerapachyinae is evidently due to two principal factors: (1) differences in ecology; for example, Kandavu and Vanua Levu are so extensively cultivated as to support smaller indigenous faunas; (2) simply incomplete collecting, which undoubtedly accounts in large part for the seeming paucity of the Halmahera, Bismarcks, and Rennell faunas.

If only those islands are considered which are along the main line of the Sunda-Melanesian arc, which still possess large tracts of native vegetation,

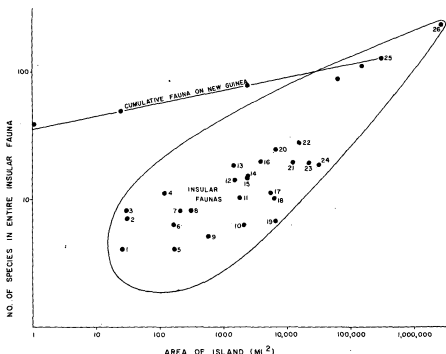


FIGURE 1. The relationship of area to number of ponerine and cerapachyine ant species in the faunas of various Moluccan and Melanesian islands. 1. Ternate; 2. Malapaina; 3. Ugi; 4. Florida; 5. Kandavu; 6. Taviuni; 7. Ndeni; 8. Amboina; 9. Rennell; 10. Vanua Levu; 11. Espiritu Santo; 12. San Cristoval; 13. Santa Isabel; 14. Malaita; 15. Waigeo; 16. Viti Levu; 17. New Hebrides (entire); 18. Ceram; 19. Halmahera; 20. Fiji (entire); 21. New Britain; 22. Solomons (entire); 23. Bismarcks (entire); 24. Moluccas (entire); 25. New Guinea; 26. central tropical Asia. The cumulative New Guinea localities given in the upper curve are as follows: lower Busu River; triangle formed by the lower Busu River, Didiman Creek, and Bubia; all of the Huon Peninsula; northeast New Guinea; northeast New Guinea plus Papua; all of New Guinea.

and which have been reasonably well collected, a much stronger correlation appears, with a slope ( $k$ ) of about 0.6 and an origin ( $b$ ) of between two and three. If literally true, this would mean that an island one square mile in area can hold only two or three species, while one under one-tenth of a square mile could hold only one species. These predictions fit very closely the actual faunal size of very small islands in Polynesia, which has been better analyzed (Wilson and Taylor, ms.).

From the details of this analysis, an interesting fact emerges: the size of individual faunas is not correlated with their nearness to the source areas of tropical Asia and New Guinea. Intuitively, one might expect the Moluccas, which are main stepping stones of faunal movement to and from New Guinea, to have a larger fauna than the more remote, peripheral Solomons and Fiji. Yet the reverse is true. The best collected Moluccan Islands (Ternate,

Amboina, Ceram) have somewhat sparser faunas than the best collected parts of the Solomons and Fijis. It is true, on the other hand, that the number of phylogenetic stocks (that is, species groups) declines significantly from the Moluccas and New Guinea eastward. But the total number of species does not deviate from the expected. On Fiji a relatively small number of stocks have diversified to "fill" the Fijian "quota."

The data suggest that individual insular faunas approach upper limits set by the size of the islands. In other words, they are in a saturated or near-saturated condition. It can be inferred that, as a rule, new species can invade an island only if resident species are extinguished to make room for them. Other lines of evidence support this generalization. In New Guinea lowland rain forests, common native ant species show patchy distributions that are poorly correlated with habitat and which result in a limitation of size of local faunas (Wilson, 1958b). In coconut plantations of the Solomon Islands, mixed populations of native and introduced species show clear-cut mosaic distributions determined less by vegetation than by interaction and replacement of competing species (E. S. Brown, 1959). The process of replacement usually involves intercolonial fighting, and it strictly limits the size of faunas of small sample areas. The phenomenon is not unique. Segregation of species by competition in the British ant fauna has already been well demonstrated in the studies of Brian (1952, 1955, 1956a, 1956b).

It is reasonable to expect that the tendency toward mosaic distributions will result in a pattern of fixation-versus-elimination of competing species on very small islands. In Polynesia, where data are now complete enough to allow a reasonably full analysis (Wilson and Taylor, ms.), this proves to be the case. The mosaic pattern is extended to include entire islands and even archipelagoes. On the major islands of Melanesia and Polynesia, and on islands as small as Nuku Hiva and Hiva Oa, members of the same species groups commonly exist together. But among yet smaller islands, such as Roruma, Raratonga, and Fakaofu, related species tend to exclude one another in an unpredictable manner, forming mosaic patterns. On still smaller islands, intergeneric replacement is evident. The latter phenomenon is consistent with the findings of Brown, who observed intergeneric strife and replacement as a common occurrence in the coconut plantations of the Solomons. As a result of this phenomenon of small-faunal diversification, the summed faunas of entire archipelagoes are larger than could be predicted from knowledge of a limited sample of individual insular faunas. As noted already, a similar process operates at the level of local faunas of large islands to enrich the total insular fauna. The phenomenon can be conveniently referred to as *faunal drift*. This expression is used simply to infer that the composition of small local faunas varies in an unpredictable manner, that is, there is a subjective element of randomness. It remains to be seen to what extent faunal drift is really the result of chance phenomena such as accidents of colonization.

We can next inquire whether faunal drift results in the stabilization of local faunal size, with the result that local faunal size, that is, the number

of species occurring in a set sample area, is independent of island size and hence of the total number of species occurring on the island. It turns out that this is not the case. As shown in figure 2, local faunal size increases with the area of the island. Local fauna here is defined as the fauna of an area of approximately one square mile (2.5 km.<sup>2</sup>) in the lowlands, and encompassing both rain forest and marginal habitats.

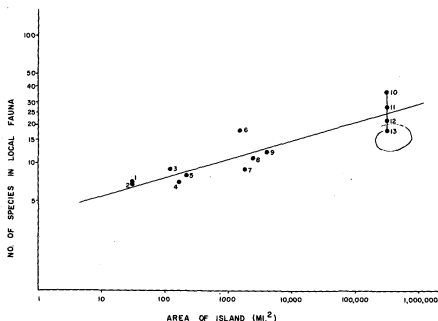


FIGURE 2. The relationship of the area of Melanesian islands to the number of ponerine and cerapachyine species occurring within local faunas on them. The following local faunas are given: 1. Pawa, Ugi; 2. Malapaina; 3. Tulagi, Florida; 4. Somo Somo, Taveuni; 5. Graciosa Bay, Santa Cruz; 6. Fulakora, Santa Isabel; 7. Luganville, Espiritu Santo; 8. Auki, Malaita; 9. Nadarivatu, Viti Levu; 10-12. localities on New Guinea.

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With respect to total faunal size in Melanesian ants, the following generalization holds: when the total number of species occurring on an island does not exceed ten species, all of them can be expected to occur in the local fauna, as just defined. When the total fauna includes about 20 species, the local fauna contains from approximately half to all of them. When the total fauna contains over 100 species (New Guinea), local faunas contain only between ten and 30 per cent.

As the sample area on a great island such as New Guinea is progressively decreased, the decrease in local faunal size is less marked than that in decreasing sample areas comprising whole islands (figure 1). Thus the level of "saturation" is higher in local faunas of large islands than in small ones.

## THE SOURCES OF THE EXPANDING SPECIES

Two geographical criteria have been used in this study to estimate the origin of a given expanding species: (a) primarily, the center of the present range of the species, and (b) secondarily, the site of maximum diversification and geographical center of the ranges of its closest relatives. In practice the two predicted centers nearly always coincide, at least to the nearest two adjacent archipelagoes. Following are examples of several of the most diverse distribution patterns that have been encountered and the decisions made about them.

(1) *Diacamma rugosum*. Ranges continuously from India to New Guinea. Two distantly related endemic species occur in the Moluccas but the great bulk of the genus occurs in the Oriental Region and is actively speciating and spreading from there. Estimated origin: Oriental Region.

(2) *Odontomachus tyrannicus*. Occurs over most of New Guinea and in the peripheral islands of New Britain, Japan, and Waigeo. The closest related species are limited to New Guinea. Estimated origin: New Guinea.

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(3) *Odontomachus saevissimus*. Occurs continuously from the Moluccas to New Britain. A closely related species, *emeryi*, is endemic to the Solomons. Speciation of other members of the *saevissimus* group is active in both the Oriental Region and in New Guinea, but primarily in the latter. Estimated origin: New Guinea.

(4) *Odontomachus simillimus*. Occurs continuously from Ceylon through most of Polynesia. The three most closely related species occur in New Guinea; one, *cephalotes*, has spread to offshore islands from New Guinea. Estimated origin: New Guinea.

(5) *Platythyrea parallela*. Ranges more or less continuously from Ceylon to Samoa and occurs (introduced by commerce) in the Society Islands. The bulk of the genus occurs in the Oriental Region. Only one other species, *quadridenta*, is native to Melanesia; this is very distinct from *parallela*, being related to the Oriental *sagei*. Estimated origin: Oriental; questionable.

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(6) *Ponera biroi*. Widespread on New Guinea, occurs in addition on New Britain and in the Solomons. A closely related species, *eutrepta*, is limited to Fiji, but the other three members of the *biroi* species group are endemic to New Guinea. Estimated origin: somewhere in New Guinea plus Bismarck; New Guinea is the more likely specific source, but both archipelagoes should be included jointly in statistical measures of faunal origins.

The patterns of distributions of several ant subfamilies in Melanesia are summarized in figure 3. Here are presented the limits of distribution of species centered in Melanesia. Those judged to be penetrating from the Oriental Region are omitted. It will be noted that the centers of distribution of the great majority of these Melanesian species are in New Guinea or, at most, New Guinea plus the Bismarck Archipelago. From this center species can be observed in virtually every stage of expansion, some reaching only to immediately adjacent archipelagoes, others outward beyond the Moluccas and Fiji. The ranges tend to be equiformal, that is, extending in both direc-

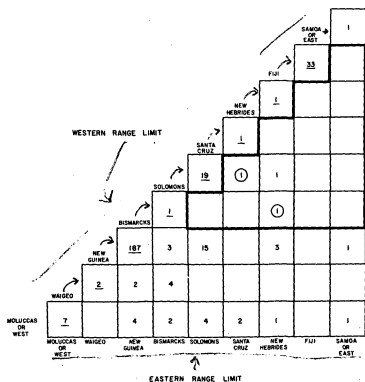


FIGURE 3. Range limits of Melanesian species of Ponerinae, Cerapachyinae, Dolichoderinae, Pheidole, Crematogaster, and Strumigenys. The number of endemic species on each archipelago is underscored.

tions from New Guinea, and in the sum their limits form concentric rings centered on New Guinea. The pattern in the vicinity of Fiji is notably different. Although 33 species are endemic to Fiji, not a single species extends from there to adjacent archipelagoes. There is, in striking contrast to New Guinea, no sign of the movement of species originating on Fiji outward from that archipelago. The Solomons fauna presents a similar pattern to that around Fiji; although being closer to the complex fauna of New Guinea, it is more difficult to analyze. Three species extend from the Solomons to immediately adjacent archipelagoes. Two, however, are evidently relicts: *Anochetus isolatus*, which is a member of a fragmented and evidently receding superspecies (Wilson, 1959b), and an undescribed species of *Crematogaster* (*Orthocrema*), which is known only from Espiritu Santo and New Ireland. The third species, *Turneria pacifica*, is classified as originating in the Solomons. The percentage of autochthonous expanding species is still much smaller in the Solomons than in New Guinea, or even New Guinea and the Bismarcks measured jointly.

In table 1 is presented an analysis of the differences in contributions of expanding species of New Guinea, the Solomons, and the Fiji. It will be

TABLE 1  
The relation of land area to percentage of expanding species in the resident fauna

Taxa included	Opposed land masses	Number of endemic species	Number of autochthonous expanding species	Difference in frequencies of expanding species	$\chi^2$	P	$\chi^2$	Pc	Statistical interpretation of frequency difference
Ponerinae,	New Guinea	187	35	0.108	1.59	0.20	0.86	0.30	Not significant
Cerapachyinae,	Solomons	19	1						
Dolichoderinae,									
Myrmicinae									
Ponerinae,	New Guinea	187	35	0.158	5.86	0.02	4.61	0.03	Significant
Cerapachyinae,	Fiji	33	0						
Dolichoderinae,									
Myrmicinae									
Ponerinae,	New Guinea plus	191	32	0.143	5.25	0.02	4.02	0.04	Significant
Cerapachyinae,	Bismarcks								
Dolichoderinae,	Fiji	33	0						
Myrmicinae									
All ant species	New Guinea plus	...	...	(0.120)	6.25	0.01	5.79	0.02	Significant
	Bismarcks								
	Fiji	58	1						

The frequencies of expanding species originating from Melanesian archipelagoes of different areas are compared. The larger proportion of such species originating from New Guinea is significant at the 95 per cent confidence level with reference to Fiji but not with reference to the Solomons, because of the smaller sample of species from the latter islands. In the last two rows New Guinea and Bismarcks are combined to give the lowest possible estimate of autochthonous expanding species. In the last row the composition of the total Fijian ant fauna is given; that of the total New Guinea-Bismarcks fauna cannot be directly estimated and is assumed to be the same as in the better analyzed taxa, comprising approximately 50 per cent of the species. Both  $\chi^2$  and Yates' correction of  $\chi^2$  for assumed continuous distribution are given.



noted that whereas approximately 15 per cent of the New Guinea (or New Guinea plus Bismarcks) fauna has expanded to adjacent archipelagoes, none of the Fijian species have, and only one, or five per cent, of the Solomons fauna can be considered to have done so. The difference between the New Guinea and Fijian faunas is significant at the 95 per cent level. That between the New Guinea and Solomons faunas is not significant, but this could be attributed simply to the smaller available sample.

TABLE 2  
The relation of land area to percentage of contributed interpenetrating species in the Ponerinae and Cerapachyinae

Competing faunas	Per cent share of land mass	Per cent share of native species	Per cent contribution of interpenetrating Stage-I species	$\chi^2$	$\chi^2_c$	$\frac{P}{P_c}$	Statistical interpretation
Fiji vs. New Guinea	2.28	16.10	$\frac{0}{1} = 0$	...	...	$\frac{...}{>0.50}$	Not significant
Fiji vs. central tropical Asia	0.25	9.44	$\frac{0}{2} = 0$	...	...	$\frac{...}{>0.50}$	Not significant
Solomons vs. New Guinea	5.22	17.76	$\frac{0}{9} = 0$	...	0.86	$\frac{...}{ca. 0.30}$	Not significant
Solomons vs. central tropical Asia	0.57	10.50	$\frac{0}{10} = 0$	...	0.60	$\frac{...}{ca. 0.40}$	Not significant
New Guinea vs. central tropical Asia	10.93	35.21	$\frac{2(\times 100\%)}{18} = 11.11$	4.40	3.40	$\frac{0.04}{0.06}$	Significant

The ponerine-cerapachyine faunas of opposing pairs of land masses are compared with reference to the exchange between them of interpenetrating species. No significant difference exists between the share of land mass and share of interpenetrating species. The  $\chi^2$  and probability values apply to the difference between percentage share in combined native faunas and percentage share in combined interpenetrating species. In the case of New Guinea (versus central tropical Asia) the difference is significant at the 95 per cent confidence level. Samples of species from other Melanesian islands are too small to allow a formal test, but even so it will be noted that the contribution of interpenetrating species by the smaller archipelagoes is consistently nil. (See also figure 4.)

We may now turn to another index of faunal dispersal, the degree to which species of one fauna penetrate other faunas. The *interpenetration* of competing faunas is measured simply as the number of species extending from one archipelago and colonizing another. Here it is possible to compute not only the exchange of faunas within Melanesia but also that between Melanesia and tropical Asia. In table 2 are given the known amounts of interpenetration.

tration within the Ponerinae and Cerapachyinae of central tropical Asia, New Guinea, the Solomons, and Fiji. These measures are coupled with land mass and total faunal size and the correlations shown graphically in figure 4. It will be seen that the percentage contribution of interpenetrating species of a given archipelago is nearly the same as its percentage share of the land mass. Note that it is theoretically possible, and interesting, to substitute percentage share of population size for percentage share of land mass. The contribution of interpenetrating species is not linearly correlated with percentage share of total faunal size, as one might intuitively expect. The dif-

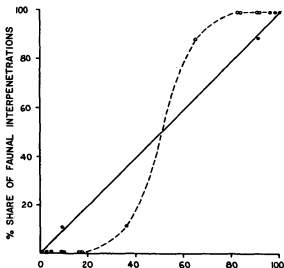


FIGURE 4. The correlation of share of interpenetrating ponerine and cerapachyine species with share of land area (solid circles and line) and with share of total number of species in competing pairs of archipelagoes (open circles and dashed line). See also table 2 and further explanation in the text.

ference between these two measures is significant at the 95 per cent level in the case of New Guinea versus central tropical Asia. A formal statistical difference cannot be demonstrated in the case of the smaller archipelagoes, due to smallness of sample size. But the relationship is numerically absolute in each case, that is, the contribution of interpenetrating species of the smaller archipelagoes is zero.

Faunal interpenetration is here defined as a direct indicator of faunal dominance. This interpretation is clarified if we consider what the joint contributions would be to an intermediate island of exactly equal accessibility. The faunas of the two source archipelagoes would "compete" to fill the island's faunal quota. It can be inferred that their percentage share of faunal contributions would be the same as the percentage share of interpenetrating species exchanged between them.

## BIOLOGICAL CHARACTERISTICS OF EXPANDING SPECIES

The Melanesian ant fauna appears to stem almost exclusively from species moving out of three source areas: tropical Asia, New Guinea, and Australia. In most of the analyses to follow, only the Ponerinae, Cerapachyinae, and selected myrmecine genera will be considered. All of the expanding species in these taxa are either Asia- or New Guinea-based, simplifying the procedures. It may be noted that Australia-based expanding species in the Dolichoderinae appear to conform to the general biological characterizations to be described in the other groups.

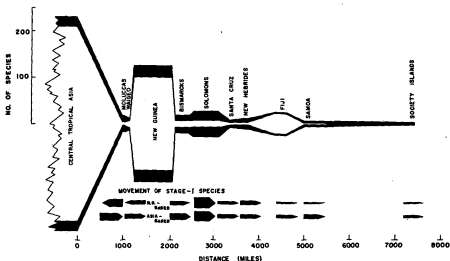


FIGURE 5. The partition of ponerine-cerapachyine species of various archipelagoes into Stage I (shaded) or Stage II and III (blank). The Stage-I species are further distinguished as Asia-based or New Guinea-based.

In figure 5 are given the partitions of some of the faunas of major Oriental-Pacific archipelagoes into speciation stages. A significant characteristic can be seen on inspection: the absolute number of Stage-I (expanding) species does not vary greatly from island to island. What varies markedly is the proportion of Stage II and III species (endemics or near-endemics). As the size of the island decreases, the absolute number of Stage-I species declines only slowly, while that of Stage II and III species declines rapidly. On islands the size of Waigeo and Ndeni (Santa Cruz) in the main Melanesian arc, Stage-I species predominate (figure 6). Fiji shows the same negative correlation between island size and proportion of Stage-I species, but the proportionality remains overall much lower.

As shown elsewhere (Wilson, 1959a) the expanding (Stage-I) species in New Guinea occur preponderantly in marginal habitats. Marginal habitats are defined as those containing the smallest number of ant species. They

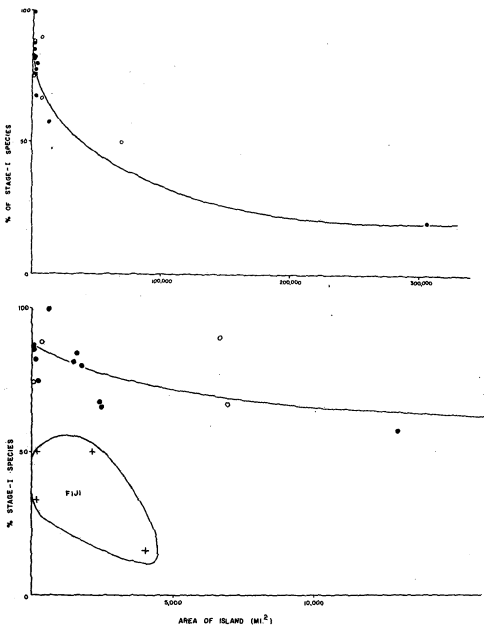


FIGURE 6. The percentage of Stage-I ponerine-cerapachyine species on islands with various areas. Open circles: Moluccas and Celebes. Closed circles: Melanesia exclusive of Fiji. Crosses: Fiji.

include the littoral zone, savannah, monsoon forest, and "open" rain forest. Stage-I species also occur in a significantly wider range of major habitats. In a later section (p. 186) it will be shown that in comparison with members of endemic Melanesian genera and subgenera, the Stage-I species *as a group*

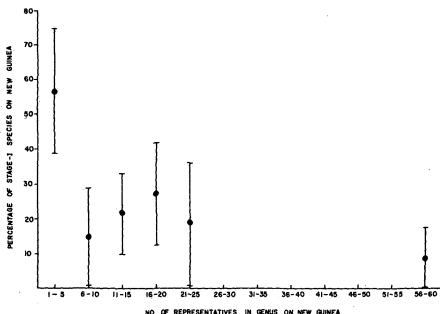


FIGURE 7. The relation of frequency of Stage-I species to size of the genus on New Guinea. The frequency of all genera combined in each size class is given, along with the 95 per cent confidence limits. The subfamilies included are the Ponerinae, Cerapachyinae, and Myrmicinae.

show greater latitude in nest-site choice and colony size. It is further the author's subjective impression, based on too few data to analyze quantitatively, that *individual* Stage-I species show relatively wide latitude in nest-site choice, but not in colony size.

It would be of interest now to inquire further into the conditions under which expanding species originate and spread. A valuable new clue is provided by the fact that a negative correlation exists between the size of the genus and the percentage of Stage-I species in the genus. As shown in figure 7, genera containing less than six species have a significantly higher percentage, about 58 per cent, of Stage-I species. Moreover, the number of Stage-I species that a single genus contains at the present time is correlated with the size of the genus but approaches a strict limit. As shown in table 3 and figure 8, even the largest genera (*Pheidole*, *Crematogaster*, *Strumigenys*, *Odontomachus*) have been able to generate no more than three Asia-based Stage-I species or four New Guinea-based ones. Further, there is a limit to the number of Stage-I species of any genus that coexist on a single island. On the largest of the Melanesian islands, New Guinea, only the dolichoderine genus *Iridomyrmex* has as many as seven Stage-I representatives. *Iridomyrmex* is exceptional in being Australia-based and in having Stage-I species conspicuously successful around human settlements. The largest ponerine and myrmicine genera have no more than five Stage-I representatives on New Guinea.

TABLE 3

Some faunal characteristics of ponerine, cerapachyine, myrmicine, and dolichoderine genera occurring in tropical Asia and Melanesia. Further explanation in the text.

Genus	No. of species in central tropical Asia	No. of species originating in central tropical Asia	No. of Stage-I species originating in central tropical Asia	No. of species in New Guinea	No. of species originating in New Guinea	No. of Stage-I species originating in New Guinea	No. of Stage-I species present on New Guinea from all sources	Presence of endemics in other faunal regions
Amblyopone	7	7	0	1	0	0	1	+
Prionopelta	1	1	1	2	2	1	1	+
Myopopone	1	1	1	1	0	0	1	-
Mystrium	1	1	1	1	0	0	1	+
Rhytidoponera	0	0	0	12	12	1	1	+
Gnamptogenys	12	12	0	6	6	0	0	+
Proceratium	2	2	0	1	1	0	0	+
Discothyrea	2	2	0	1	1	1	1	+
Leptogenys	25	25	2	13	12	1	3	+
Anochetus	21	21	1	6	5	1	2	+
Odontomachus	8	8	2	17	14	3	5	+
Platythyrea	7	7	1	2	1	0	1	+
Bothropoponera	19	19	1	2	?	?	?	+
Ectomomyrmex	13	13	0	6	6	1	1	-
Centromyrmex	1	1	0	0	0	0	0	+
Cryptopone	2	2	2	4	2	1	3	+
Diacamma	11	11	1	1	0	0	1	-
Emeryopone	1	1	0	0	0	0	0	-
Brachyponera	4	4	1	2	1	1	2	+
Mesoponera	2	2	0	2	2	1	1	+
Trachymesopus	4	4	2	3	1	1	3	+
Ponera	30	30	2	20	18	3	5	+
Pseudoponera	2	2	1	0	0	0	0	-
Myopias	6	6	0	14	14	0	0	-
Haepgnathos	2	2	0	0	0	0	0	-
Odontoponera	1	1	1	0	0	0	0	-
Cerapachys	12	12	0	9	9	1	1	+
Phyracaces	5	5	0	2	2	0	0	+
Lioponera	2	2	0	1	1	0	0	-
Simopone	2	2	0	0	0	0	0	-
Sphinctomyrmex	?	?	?	?	?	?	?	+
Crematogaster	70	70	1	26	25	4	5	+
Pheidole	81	81	2	58	56	4	5	+
Strumigenys	16	16	1	21	20	3	4	+
Hypoclinea	20	20	1	1	0	0	1	+
Monoceratoctinea	0	0	0	2	2	0	0	-
Leptomymex	0	0	0	3	3	1	1	+
Technomyrmex	10	10	1	2	1	0	1	+
Turneria	1	?	?	3	3	1	1	-
Iridomyrmex	1	0	0	13	8	2	7	+

In seeking an explanation for this phenomenon, we may look directly to the role of interspecific competition. There is excellent additional evidence to favor the hypothesis that competition is decisive. The Stage-I species on New Guinea include no closely related pairs. Stage-I species in the same

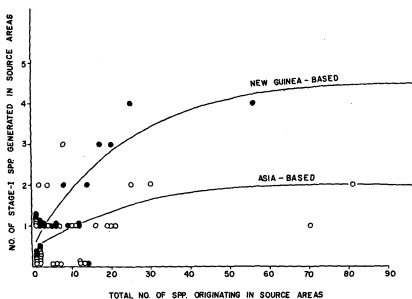


FIGURE 8. The relation of size of genus to number of contained Stage-I species in the Ponerinae, Cerapachyinae, and Myrmicinae in Asia (open circles) and in New Guinea (closed circles). Note that no genus has been able to generate more than four Stage-I species from one source area. See also table 3 and further explanation in the text.

genus tend to be markedly different from one another in morphology, ecology, and behavior. In most cases where the same broad species group is represented by more than one Stage-I member, for example, *Odontomachus simillimus* with *O. cephalotes*, *O. malignus* with *O. saevissimus*, the members occur in different major habitats. Additional supporting evidence is found in the phenomenon of *ecological release*: although the Stage-I species tend to be restricted to marginal habitats on New Guinea and Fiji, which have large endemic faunas, they are not so restricted in the more depauperate Solomon Islands and New Hebrides. On Espiritu Santo, where the author conducted field studies, several Stage-I species, for example, *Odontomachus simillimus*, *Pheidole oceanica*, *P. sexspinosus*, *P. umbonata*, were among the dominant ant species in deep virgin rain forest. At lowland stations on New Guinea, the same species were much sparser and limited to marginal habitats. Other Stage-I species that have marginal distributions on New Guinea, including *Rhytidoponera araneoides*, *Iridomyrmex cordatus*, and *Oecophylla smaragdina*, are dominant in the rain forests of the Solomon Islands (Mann, 1919). There can be no question that interspecific exclusion underlies this phenomenon. Suitable nesting sites and trophophoric fields are virtually saturated with ant colonies in both New Guinea and outer Melanesia. Where large native faunas exist, there is literally no room for significant populations of Stage-I species. Reference has already been made to the role of direct colony conflict in interspecific exclusion of Stage-I ant introduced spe-

TABLE 4

Asia-based genera				New Guinea-based genera			
Represented in other faunal regions				Represented in other faunal regions			



Adelomyrmex (*Arctomyrmex*), *Aphaenogaster* (*Planimyrmex*), *Ancyridris*, *Dacetinops*, *Arnoldidris*, *Archaeomyrmex*, *Willowsiella*, *Poecilomyrma*, *Crematogaster* (*Rhachiocrema*), *Crematogaster* (*Xiphocrema*), *Pheidole* (*Electropheidole*), *Pheidole* (*Pheidolacanthinus*), *Monoceratoclinea*, *Mesoxena*, *Camponotus* (*Myrmegonia*), *Camponotus* (*Condylomyrma*), *Polyrhachis* (*Dolichorhachis*). Endemic Melanesian taxa generally contain a relatively small number of species limited to one of the three following archipelagoes: New Guinea, Solomons, and Fiji. It is not possible to determine whether they are relicts or autochthonous taxa at maximum range. (New Caledonia, which has a virtually independent ant fauna derived from Australia, is not considered here.)

In contrast with the above set of taxa are genera and subgenera, headquartered in tropical Asia or tropical Asia plus New Guinea, which are generating Stage-I species and are not notably disjunct. These include *Aenictus*, *Mystrum*, *Leptogenys*, *Anochetus*, *Odontomachus*, *Platythyrea*, *Cryptopone*, *Diacamma*, *Brachyponera*, *Trachymesopus*, *Ponera*, *Pseudoponera*, *Odontoponera*, *Cardiocondyla*, *Crematogaster* (*Orthocrema*), *Strumigenys*, *Rhopalomastix*, *Calyptomyrmex*, *Pheidole* s. str., *Pheidologeton*, *Monomorium*, *Vollenhovia*, *Tetramorium*, *Hypoclinea*, *Technomyrmex*, *Pseudolasius*, *Paratrechina* (*Nylanderia*), *Oecophylla*, *Camponotus* (*Dinomyrmex*), *Camponotus* (*Myrmamblys*), *Camponotus* (*Colobopsis*), *Camponotus* (*Tanaemyrmex*), *Polyrhachis* (*Polyrhachis*), *Polyrhachis* (*Chariomyrma*), *Polyrhachis* (*Myrma*), *Polyrhachis* (*Myrmhopla*).

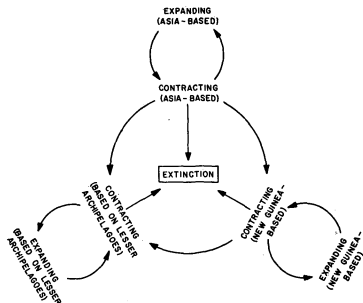


FIGURE 9. The taxon cycle in Melanesian ants. The following features are postulated: the taxon can undergo alternate expansion and contraction, with or without speciation, for an indefinite period of time; it can shift its headquarters from a large land mass to a smaller one but not in the opposite direction.

For convenience, the relative evolutionary positions of the two sets of taxa can be classified as "contracting" and "expanding" in the simple dichotomy represented in figure 9. Taxa endemic to the Solomons or Fiji can be safely regarded as either contracting or at least permanently confined, according to the evidence previously discussed. Taxa endemic to or centered on New Guinea with relicts outside may either be retreating or potent, that is, destined to expand; it is not feasible to speculate further on this

TABLE 5

Characteristic	Expanding taxa			Receding or autochthonous taxa			$\chi^2$	p	$\chi^2_c$ *	$p_c$ *	Statistical interpretation
	+++	++	+	+++	++	+					
Spinescence	3	33	1	12	5	1	20.93	<0.0001	18.04	<0.0001	Highly significant
Cryptobiosis of non-spinescent forms	5	...	26	3	...	2	3.99	0.04	2.59	0.10	Doubtfully significant
Colony size	3	10	3	0	2	4	6.70	0.01	4.14	0.04	Significant
Terricolous species: small log nest site	5	...	18	4	...	1	6.40	0.01	4.00	0.04	Significant
Prominent use of odor trails	10	...	16	0	...	8	4.36	0.04	2.70	0.10	Doubtfully significant
Species limited chiefly to the mid-mountain rain forests	1	...	31	6	...	6	12.04	<0.001	9.29	<0.001	Highly significant
Species limited entirely to inner rain forest habitats	7	...	23	13	...	2	16.25	<0.001	14.01	<0.001	Highly significant

\* Yates—corrected for continuity.

Some biological differences between expanding genera and confined (retreating or autochthonous) genera in Melanesia. Each qualitative characteristic has been classified as present (+++) or absent (+). Continuously varying characteristics have been roughly classified quantitatively into three classes. Colony size is based on estimates given in Wilson (1959d) and is partitioned into three groups with adult populations of 90 or less (+), 100-800 (++), or 1000 or greater (+++). Not all taxa were well enough known to classify with respect to each characteristic. Only characteristics are shown in which these differences between the two sets of taxa are significant at the 95 per cent confidence level.

distinction. In any case, it is clear that the two sets of taxa belong to different major stages in cyclical evolutionary development in the Oriental-Melanesian fauna (Wilson, 1959a). We may now raise the following question: do taxa undergo parallel biological changes correlated with these zoogeographic episodes? To explore this possibility, the two groups of taxa were scanned for biological differences among diverse morphological, ecological, and behavioral characters. Certain differences were found, as shown in table 5. Background information concerning most of these characters, apart from their evolutionary classification, has already been presented in earlier papers (Wilson 1959a, b).

## DISCUSSION: A THEORY OF THE TAXON CYCLE

Enough zoogeographic and ecological data have now been accumulated to justify a preliminary reconstruction of the generalized taxon cycle of the Melanesian ant fauna. Let us start with the actual process of speciation. The evidence suggests that the chief geographic barriers are the water gaps. Speciation probably occurs by internal fragmentation of some populations on the great island of New Guinea, but this appears to be a minor phenomenon, principally involving retreating endemic species. As a rule, semispecies and superspecies, comprising the populations at the threshold of speciation, break at the water gaps. Furthermore, the wider the water gaps, the more frequent the breaks between the allopatric populations. Finally, accumulations of related species on single archipelagoes or islands is chiefly the result of multiple invasions (Wilson, 1959a).

Expanding species in Melanesia originate almost entirely from tropical Asia, New Guinea, and Australia. These are moreover the "potent" species that must from time to time give rise to new taxa. However, the fossil record reveals that ant evolution has been relatively conservative since the early Tertiary (Wheeler, 1914; Carpenter, 1931). The zoogeographic evidence indicates that the origin of new potent taxa of higher rank is a rare event in tropical Asia and Melanesia. Among the 41 smaller ant genera confined to tropical Asia and New Guinea, only three (Myopopone, Odontoponera, Pseudoponera) contain expanding species. Of 51 ant genera of comparable representation in tropical Asia and New Guinea but with representation in other faunal regions (hence, older genera?), 17 contain expanding species. (See table 3.) Other distinctive endemic genera have been evolved in the Solomons, Fiji, and New Caledonia but are strictly limited in size and show no sign of extending their ranges. Thus, the origination of higher taxa is a relatively common event in the Oriental-Melanesian region, but the new products are usually strictly limited to the archipelagoes in which they are born. The combined evidence indicates strongly that the creation of the occasional potent new genera and higher taxa is confined to the large source areas of tropical Asia and New Guinea. Indeed, since Myopopone, Odontoponera, and Pseudoponera are all Asia-based, it is possible that tropical Asia alone serves as a significant source area of potent taxa higher than the species group. Retreating taxa can shift their headquarters from larger to smaller land masses but not in the opposite direction (figure 9).

At lower taxonomic levels, the ants seem to conform to the rule expressed earlier by Darlington (1957, 1959) for vertebrates, that dominant taxa tend to arise in and spread from the largest favorable land masses. It is possible to go a step further and specify that in Oriental-Melanesian ants, the degree of faunal interpenetration is closely correlated with land mass and only secondarily correlated with faunal size, as shown in figure 4.

There is good reason therefore to focus special attention on the ecology of the large land masses generating Stage-I species: tropical Asia and New Guinea. From our somewhat more advanced knowledge of the New Guinea

fauna, the following generalization can safely be made. Stage-I species are being produced under conditions of intense and complex competition. As a prelude to expansion out of New Guinea, they became adapted to a wide variety of marginal habitats, containing sparse ant faunas. They are excluded for the most part from the rich inner rain forest habitats by variable numbers of endemic species ecologically similar to them. The endemic competitors are characterized by a high degree of specialization correlated with a more complex partitioning of the environment (Wilson, 1959d) and by smaller individual populations. On other Melanesian islands with depauperate endemic faunas, Stage-I species penetrate the inner forest, mount dense populations there, and fill the available nesting sites.

From the evidence concerning ecological release, the following general prediction can be made: the ecological amplitude of both expanding and endemic species should be negatively correlated with the size of the island on which they occur and hence with the size of the local fauna to which they belong. This prediction cannot be rigorously tested at the present time, but it does seem to be supported by some additional evidence concerning increased variation in morphology of Fijian *Poneræ* (Wilson, 1958a, p. 344) and in feeding habits of Fijian *Strumigenys* (Brown and Wilson, 1959, p. 289).

Species centered in the marginal habitats of New Guinea have greater opportunities for dispersal. They are poised along the coast and river banks which are the best points of departure for neighboring islands. The smaller corridor islands that can be used as stepping-stones possess the same simplified environments, both physical and biotic, that characterize the marginal habitats on New Guinea.

As the island stepping-stones decrease in size, the percentage of Stage-I species in their faunas increase (figure 6). All of the islands of the Sunda-Melanesian arc, with the possible exception of Fiji, support a strong complement of Stage-I species. On small and medium islands there is therefore a significant constriction of older faunal elements (figure 5). It can be deduced that since the number of Stage-I species does not vary greatly according to islands, the turnover of Stage-I species will probably not vary greatly either. But since the number of older (Stage II and III) species decreases markedly with decrease in island area, we can expect Stage-I species to replace them faster on smaller islands. This prediction seems to be verified by the pattern of distributions of disjunct species groups in Melanesia. As a rule, disjunction involving a hiatus of one or more archipelagoes occurs only after the refugium populations have diverged to species level. This is best interpreted as a result of the fact that speciation ordinarily occurs as the taxon retreats into the inner forest habitats, evidently under displacement pressure from Stage-I species (Wilson, 1959a). Taxa disappear first from the smaller islands and then, apparently progressively, from larger islands. The oldest and most divergent members of disjunct taxa are concentrated as relicts on the largest islands, for example, on New Guinea, the larger Solomons, and Viti Levu. Within the hiatuses the disjunct taxa are commonly represented by ecological vicars from other taxa which are con-

spicuously abundant and widespread ("ecologically released" species). The following example is unusually clear-cut. Several *Iridomyrmex* species utilize rubiaceous ant-plants of the genera *Myrmecodia* and *Hydnophytum* as their chief nesting sites. On New Guinea these plants are occupied primarily by *I. cordatus* in the marginal habitats and by *I. scrutator* in the inner forest. The ant-plants are saturated by ant colonies and the replacement is therefore virtually absolute. In the Solomon Islands *scrutator* is absent, and *cordatus* is abundant in both marginal habitats and the inner forest. On Fiji *cordatus* is absent, and the ant-plants are occupied by a third species, *nagasaui*, which is closely related to *scrutator* and presumably cognate with it.

In summary, expanding (Stage-I) species in Melanesia originate almost entirely from tropical Asia, New Guinea, and Australia. Consequently, these land masses have probably been the ultimate source of all new taxa generated in the Indo-Australian Region and the immediate source of all potent new taxa. The Stage-I species evidently serve an important additional role in displacing, fragmenting, and directing the evolution of older resident species. It can be added that the taxon cycle dates no further back than the early Tertiary, when the radiation of modern ant genera began. Throughout the Cenozoic Melanesia has been broken into numerous islands, at least intermittently (Umbgrove, 1949; Derrick, 1951; Grover, 1955), thus facilitating speciation by multiple invasions. In Miocene times, the Solomon and Fiji Islands were mostly submerged. The evolution of the modern ant fauna of these islands may not date beyond this epoch. The Fijian fauna especially has a modern cast, with no indisputably ancient representatives among its endemic taxa.

A major attribute of evolutionary success in taxa is seen to be the ability to move member species into marginal habitats, at least temporarily. By examining the expanding species we might hope to discover other biological attributes that provide success, in other words, to define new biological rules that apply to the phenomenon of "general adaptation" (Darlington, 1959). Beyond generating marginal-habitat species, however, the expanding taxa appear to be distinguished by only one other common characteristic: great diversity among themselves. In fact, as noted already, ~~one~~ <sup>only</sup> ecologically divergent elements are able to travel through the marginal-habitat channel simultaneously. From this evidence it would seem logical to conclude that general adaptation involves the acquisition of a marked ecological difference. Perhaps the larger this difference the more successful will be the taxon. But of course complete and permanent escape from the faunal equation is impossible and replacement must be inevitable, starting on the smaller islands and in the poorer habitats. Therefore, a second common quality of general adaptation is undoubtedly the ability to replace competitors in the zones of ecological overlap. Perhaps the two qualities are related as follows: the penetration of a new major niche provides the ancestral species with an unmolested population reservoir that allows it, at least for a time, to mount sufficient populations and new adaptations to usurp other niches already occupied by competitor taxa.

The endemic higher taxa, including both confined autochthons and retreating relicts, show more biological uniformity than the expanding taxa, as indicated in table 5. Individually they occur in fewer major habitats (see Wilson, 1959a, p. 137) and occupy a smaller range of nest sites. Collectively they can be characterized by other biological features that are highly variable in expanding taxa. It must be asked whether the collective features are not purely accidental, that is, random correlations derived from the scanning of a great many independent characteristics, or whether they represent a coadaptive complex correlated in some way with the declining position of the taxa in the faunal balance. In fact, most of the features do seem to be associated with the restriction of the endemic taxa to the inner forest habitat. Spinescence may not be part of the coadaptive system; this character is found in terricolous ants that forage above ground and probably serves as a protection against predators (Wilson, 1959d). It may be significant that most of the non-spinescent endemic taxa are notably cryptobiotic, that is, confined in foraging to soil cover and rotting wood. There is a strong tendency for the terricolous species to nest in small rotting logs and branches in the leaf litter; this is the preferred nest site of inner rain forest ant species generally. Colonies are relatively small, a trait closely associated with the restricting nature of the small-log nest site. Finally, odor trails are seldom if ever used, a negative characteristic generally associated with small colony size in ant species. Thus, it appears that endemic taxa are concentrated in and largely restricted to the habitats and nest sites where the greatest number of Melanesian ant species occur. The restriction is reflected in certain other adaptive characters.

If the taxon cycle described here is true for Melanesian ants, it is not necessarily true for other kinds of organisms. Ants are peculiar in several important respects: they are social, highly territorial, and so abundant as to play major roles in the ecosystems in which they live (Branner, 1912; Sernander, 1906; Tevis, 1958). As a result interspecific competition may be more important in their evolution than it is in most other groups of organisms. If the origination of potent new taxa of ants is limited to the larger land masses, this is not necessarily the case in birds (Mayr, 1954), *Drosophila* (Carson, 1955), or morabine grasshoppers (White, 1959). Indeed, the entire form of the taxon cycle may be altered in groups with markedly different ecology and population structure. It is one of the tasks of comparative zoogeography to determine the extent of this variation in histories.

#### SUMMARY

Undisturbed ant faunas of islands in the Moluccas-Melanesian arc are for the most part "saturated," that is, approach a size that is correlated closely with the land mass of the island but only weakly with its geographic location (figure 1). In the Ponerinae and Cerapachyinae combined the saturation level can be expressed approximately as  $F = 3A^{0.6}$ , where  $F$  is the number of species in the fauna and  $A$  the area of the island in square miles.

Interspecific competition, involving some degree of colonial warfare, plays a major role in the determination of the saturation curve. It deploys the distribution of some ant species into mosaic patterns and increases the diversification of local faunas. Perhaps because of the complex nature of the Melanesian fauna, differences between local faunas appear that give the subjective impression of randomness. Despite the action of species exclusion, the size of local faunas occurring within a set sample area increases with the total size of the island (figure 2).

Water gaps break populations and initiate speciation in Melanesia. Endemic insular faunas build up primarily by the process of multiple invasion.

Expanding species now on Melanesia originated almost exclusively from tropical Asia, New Guinea, and Australia. Faunal dominance, measured by the degree of faunal interpenetration, is a direct function of land area and is less directly related to insular faunal size (figure 4). Taxa originating in Melanesia exclusive of New Guinea are almost all confined to the archipelagoes of their birth.

The following taxon cycle is postulated. A taxon maintains its headquarters in a given land mass indefinitely, expanding and contracting cyclically, or else it declines to extinction. The headquarters can be shifted from a larger to a smaller land mass (for example, from New Guinea to Fiji) but not in the reverse direction (figure 9). Taxa originating in Melanesia exclusive of New Guinea are almost all confined to the archipelagoes of their birth.

On New Guinea, expanding species occur primarily in marginal habitats. In the inner rain forest habitats they are replaced by the large endemic faunas. On archipelagoes with small endemic faunas, the expanding species are ecologically "released," becoming abundant in the inner forest habitats and otherwise increasing their ecological amplitude. As a group they are characterized by great diversification among themselves. No genus among those studied has produced more than three Asia-based or four New Guinea-based Stage-I species (figure 8). No genus studied, including the largest and most successful, has a total of more than seven Stage-I species on New Guinea. Sympatric Stage-I species in the same genus tend to be ecologically and morphologically very dissimilar.

The following rule is predicted: the ecological amplitude of individual species, both expanding and endemic, should be negatively correlated with the size of the local fauna to which they belong and hence the size of the island on which they occur. The prediction is based on the phenomenon of ecological release of Stage-I species and appears to be supported by some fragmentary evidence relating to Fijian endemic species.

Expanding species evidently play a major role in the fragmentation and speciation of older taxa. By dominating the faunas of smaller islands they maintain hiatuses in the ranges of the disjunct taxa. By saturating the marginal habitats they restrict the older taxa to the inner rain forest.

Autochthonous and retreating taxa show certain common biological char-

acteristics coadaptive with restriction to the inner forest habitats. These involve nest site preference, colony size, and foraging behavior (table 5).

Three general attributes of success are recognized in the expanding Melanesian ant taxa: the acquisition of a significant ecological difference, which presumably reduces interspecific competition, the ability to penetrate the marginal habitats, and the ability to disperse across water gaps. It is suggested that the attributes are causally related in the sequence given. Success in the marginal habitats gives expanding species the advantage needed to encompass and progressively replace older resident taxa.

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